ON THE GROWTH-PERIODICITY OF THE POTATO-TUBER.[1]

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WHILE considerable research has been bestowed upon the physiology of bulbs, corms, and tubers, it does not appear that any extended observations have been made upon the method of growth of such an organ as the potato-tuber. It is a well-known fact that the growth in length of upright stems and other aërial organs is not regular, but exhibits a marked daily periodicity, the time of greatest average growth being in most cases not far from six o'clock in the morning. Upon this subject, since the researches of Sachs,[2] Baranetski,[3] Pfeffer,[4] and others, a number of observations have been made by various investigators. It appears that in most above-ground organs there is a clearly marked diurnal period, unless this period is obliterated by etiolation, suffocation, anæsthesia, or some other abnormal condition. We know, too, that besides the daily periodicity there is a grand-period of growth for each organ of the plant; that some organs reach the grand-period more rapidly or continue in it longer proportionately than other organs or similar organs on the other plant, or in the same plants under different conditions. The growth in length, then, of any organ is not regular, but is to be graphically represented as a wavy curve, with an ascending portion, a climactic portion, and a descending portion. In all of the parts of this large curve, the climax of which represents the grand-period of growth, one must notice the rhythmic pulsations due to the daily growth-periods, and more or less synchronous with the alternating periods of light and darkness, of higher and lower temperature, of less and of greater oxidation.

[1] Read before the Minnesota Academy of Science, May 5th, 1891.

[2] Arbeit. d. Würtzb. Institute, 1873.

[3] Die tägliche Periodicität d. Langenwachsthums, 1879.

[4] Physiolog. Untersuchungen, 1873.

Seasonal rhythm in the growth in girth of organs is well known in the ordinary woody stems of Dicotyledons[5] and Gymnosperms,[6] where the increasing tensions of later months reduce the rate of growth below the rate of the earlier months. This periodicity is a more simple and readily explained form than those forms which have been alluded to above. It is found principally in organs provided with a cambium cylinder and a relatively inextensible bark, and is referred to merely by way of illustration. While the potato-tuber, which is to be considered, has a cambium area, it can scarcely be said to have a cortical area at all analogous to that of the erect tree-trunk. We shall not find the tuber, protected as it is and growing during a single season, affected by the conditions of alternate freezing and thawing, wind disturbance, stress, flexion, etc., which have so much to do with seasonal periodicity of growth in girth of woody stems.

A few months ago the writer was struck with what seemed to be a great dearth of investigations into the manner of growth of tubers, and forthwith gave some attention to devising a method by which the gap in our knowledge of tuber-physiology might be filled in part. After due deliberation a method was formulated and applied, with but imperfect success at first, but as experience became wider the imperfections were gradually remedied. In all of the experiments Mr. C. P. Lommen, student in biology at the University of Minnesota, gave much assistance in setting up apparatus, and by one or two helpful suggestions concerning certain technical difficulties which presented themselves in the course of our investigations. The method of research first adopted by us has been described elsewhere somewhat in detail,[7] but upon this method certain important improvements have been made. The apparatus used was the Baranetski self-registering auxanometer, with electric clock attachment, manufactured by Albrecht, of Tübingen. At first both wheels of the apparatus were not employed, but afterwards it was found that two wheels could be combined in such a way as to multiply the tracings tenfold, and

[5] Pfeffer. Pflanzen-physiologie, II., 89.

[6] Hartig. Anat. und Phys. der Holzpflanzen, p. 366.

[7] *L. c. Botan. Gazette*, May, 1891.

in our later experiments the wheel attached to the tuber-thread does not bear the tracing needle, but carries another thread on its large circumference, which runs to the small circumference of the tracing wheel. By this means hourly registrations are obtained instead of three-hour registrations as by the first method.

To recapitulate the method as finally developed: A potato-plant, grown in a box from which one end had been removed, was selected and carried to the experimenting room. With due care a tuber was exposed, and under it, resting upon the bottom of the box, a wooden block was placed in such a way that downward pressure would not disturb the position of the tuber. The root-stock umbilicus was protected from desiccation or injury during these processes of blocking up. Next a wooden jacket consisting of two squares of cigar-box material, held together by a number of slightly stretched rubber-bands, was fitted over the tuber in such a way that one square of the cigar-box wood clung to the block below and the other piece was parallel, but on the upper side of the tuber. To the center of this upper square a small screw was fixed, and to this screw a fine silver wire was tied,—since thread was rotted by the soil,—and this wire, after the whole apparatus of block, tuber, and jacket was covered with earth again, came to the surface of the soil under the first wheel of the auxanometer. An inch and a half above the ground a twisted linen thread, which gave better friction on the wheel, was attached to the silver wire, and this twisted thread was passed over the small circumference of the first wheel and drawn taut by a weight of about forty grams. Passing from the large circumference of the first wheel to the small circumference of the second was a linen thread equally weighted at each end, and over the large circumference of the second wheel was passed a thread, bearing at one end the tracing needle and at the other a small counterpoise. The tracing needle was placed in contact with the vertical smoked cylinder of the registering apparatus. This rested upon a clock-work in which a ratchet-wheel was caught by a lever attached to the clock-work by a spring and bearing at the opposite end an armature near the poles of a small electro-magnet. Connected with the magnet was a two-celled La Clanche

battery, but interpolated in the circuit was the electric clock, so adjusted that every hour the circuit was closed for a few seconds. During the closure of the circuit the electro-magnet attracted the armature, overcoming the tension of the spring and releasing one cog of the ratchet-wheel. By this means the vertical cylinder turned about one-sixteenth of an inch with the hands of the watch, and the tracing needle made a horizontal mark upon the smoked paper covering the cylinder. The opening of the circuit as the hands passed by the hour released the armature, allowed the spring to pull back the lever, and stopped the clock-work until the next hour, when a similar horizontal mark was made. During the hours, then, any expansion of the tuber would loosen the string attached to the jacket. Pulling against this the weights would turn the first wheel. This would turn the second wheel, and the indication of growth, one hundred times magnified, but in proper ratio, would appear as vertical tracings upon the smoked cylinder. This brief description of the Baranetski apparatus is given that the exact method of research may be apparent.

The first experiments upon the growing tuber, made in accordance with the method described in the *Botanical Gazette*, were satisfactory in so far that they demonstrated the availability of the Baranetski apparatus for the purpose for which it was employed. In one of the early experiments a trace of periodic growth was distinguished, but it did not seem to be sufficient to justify any confident assertion of periodicity. The first experiment continued two weeks. During this time the needle kept falling; at the close of the experiment it was about half an inch below its original level. In the second experiment certain drops in the tracings, usually in the early morning, were noticed, but I have since come to believe that not all of these were true growth-tracings, but were due, at least in part, to changes of temperature of the soil, the strings, and the atmosphere, with consequent shortenings, relaxations, and alterations in the needle-position. Against such accidental and confusing records there was a constant necessity of guarding. In general, a conservative statement of conclusions from these experiments with the single wheel is as follows:

1. The apparatus as set up indicated growth by cylinder-tracings.

2. A possible indication of periodicity in the growth may have manifested itself.

Further than this one could not go under the conditions of the experiment.

Desiring to obtain more perfect results, and to solve the question as to the manner of growth of the tuber, the improved method of setting up the apparatus was developed as described above, and the first experiment gave some interesting results. The method of culture in water employed by De Vries[8] in the study of roots was contemplated, but rejected on account of certain practical difficulties.

The experiment began with a tuber about ¾-inch in diameter. At this time the full-sized top of the plant had begun to perish from the effects of mildew. After attachment the registering needle gave two or three sharp drops, owing to the stretching of strings and general getting into equilibrium of the apparatus. After this stage was passed the needle began dropping very gradually. This slow descent was continued from eight o'clock in the evening until about eight o'clock in the morning. At this time the drop ceased, and horizontal tracings continued until about 1.30 P. M., when a short, abrupt hour's drop was registered, followed by a longer one, then by one shorter than the second but longer than the first, next by one longer than any, closely succeeded by another long one. After this the registrations were short, and the regular, gradual fall until 8 A. M. began. Here again the horizontal mark began and continued until 2 P. M., when a second drop began, on a somewhat smaller scale than the one registered the first day. The total extent of the second day's maximum, between 2 P. M. and 8 P. M., was about one-half of the first day's maximum. The third day the same tracings continued at the same hours,—only the tracings of the maximum were very much reduced, so as to be not more than one-quarter the total length of the second day's tracings. The fourth day's tracings were like those of the second day in almost every par-

[8] *Landwirthschaftliches Jahrbuch*, 1880, Bd. IX., p. 37.

ticular, and those of the fifth day likewise, except that the latter showed a less maximum growth. The sixth day was peculiar. During this day no appreciable drop in the tracings was detected. The explanation of this cessation is not offered. It may be said, however, that the death of the top was now about complete, so far as the leaves and the secondary branches were concerned. Only in the lower part of the main stem was living green tissue to be found. During the whole twenty-four hours of the sixth day, then, no divergence of the tracings from the horizontal was observed; but during the succeeding twelve hours a slight drop began. At 7 o'clock A. M. of the seventh day a decided drop began, continuing until 11 A. M. There then succeeded a period of gradual dropping, which disappeared about 3 P. M. Another drop took place in the evening from 6 to 9 P. M. The eighth day began with a drop at 7 A. M., continuing until 11 A. M., when three hours of horizontal marks followed. At 2 P. M. a five-hour drop began, and continued as a gradual depression until 10 P. M. At 7 A. M. again another abrupt drop was registered, terminating at 11.30 A. M. At 3 P. M. a gradual, slight drop, lasting until 8 P. M., ensued. During four succeeding days the same rhythm continued, only the drops became slighter and slighter. Finally, on the fifteenth day the needle ceased to trace.

The explanation of these very curious maxima and minima in the growth of the tuber is a complicated matter. It can be given as yet only conjecturally. Before passing to any such conjectures it may be well to give in their order the conclusions arrived at from the line of research described above:

1. The increase in diameter of the potato-tuber is not regular, but is rhythmic.

2. Maxima of growth may occur either once or twice, and perhaps oftener, during twenty-four hours.

3. Maxima of growth are not of long duration, and are followed by periods of slower growth, or of entire cessation of growth.

4. The maxima of some days are greater absolute maxima than those of other days. This indicates a grand-period for the tuber.

5. Regular periodicity in the tuber continues after the periodicity of the aërial stem is suspended.

6. Connected with profound changes of condition in the aërial stem changes in the periodicity of the tuber may be noted.

7. There is some connection between the periodic growth of the tuber and the periodic growth of the aërial stem. What this connection is does not appear.

8. There is also, it is probable, an *independent* periodicity in the growth of the potato-tuber which is obscured and modified by the secondary *induced* periodicity, which is related to conditions of the aërial stem and its mode of growth.

Passing now to conjectural explanations of the observed periodic growth of the potato-tuber, it may be affirmed that very little can be expected at this stage of the investigations. Whether like embryonic shoots of Hedera, with their heliotropic irritability, the potato-tuber retains, somehow, in hereditary fashion, its above-ground periodicity, and thus gives hint of the time when its precursors were exposed to rhythmic alternation of light and darkness, is entirely an open question. On the other hand, it is equally uncertain whether the induced periodicity is due to one or many causes. Some lines of attack are indicated below, and it is hoped that they may be followed to their rational conclusion.

1. The rhythm of *assimilation* in the above-ground stem may affect the growth of the below-ground tuber. The synthesis of carbohydrates is a diurnal affair. From these carbohydrates the substance of the tuber is formed. Thus the rhythm above might induce a rhythm below.

2. The conversion of plastic into reserve materials is characteristic of an organ like the tuber. This conversion depends upon the activity of certain ferments which are results of destructive and constructive metabolic changes in the shoot area. These metabolic changes are consequent upon the *respiration* function, and this is a rhythmic function.

3. The *growth* of the above-ground stem is strongly periodic, and demands, in any plant, the same kind of material which would be supplied to a growing tuber. This drain upon the plastic material in one direction might induce a corresponding dearth of it in

another, so that the periodic growth of the above-ground stem might induce a periodic growth in the below-ground tuber.

4. The *asynchronous grand-periods* of growth of the different above-ground organs might be reflected in an irregular and erratic periodicity in the below-ground tuber.

5. *Combinations* of these various conditions, and a modification of them all by the independent rhythm of the tuber itself, would have to be considered, and only by the most elaborate and extended researches could the proximate causes for the observed tuber-periodicity be detected.

In closing this contribution to the physiology of tubers, one word may be added by way of note. It is possible, as may be shown, to apply auxanometer methods to root stocks by uncovering the root stock, attaching a silver thread, running it horizontally to the open side of the box, passing under a horizontal roller and upward, and finally adding the linen or silken thread which runs on the small circumference of the first wheel. Or, in this case, doubtless one wheel alone could be employed. Such study of underground stems, as in the grass root stock, the potato rhizome, or any other underground stem, would scarcely fail to throw some light upon the method of growth of the tuber. A comparison of underground organs should be made along this line.

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